

1. On some Points in the Anatomy of the *Columbæ*. By
A. H. GARROD, B.A., Fellow of St. John's College, Cambridge; Prosector to the Society.

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In the present communication it is not my intention to describe in detail the anatomy of any single kind of Pigeon, because that can be, most of it, learnt from the dissection of any common species; but, from the opportunities which are presented to me in the performance of my prosectorial duties, it will be my endeavour to point out those peculiarities which I have been able to recognize in the soft parts of the large number of generic forms of the *Columbæ* that have passed through my hands. It is my hope that those naturalists who have opportunities of examining genera and species which it has not been my good fortune to obtain, will record their observations, not omitting those points on which I shall endeavour to lay stress on the present occasion.

That there is not a perfect constancy in the pterylosis and visceral anatomy of the Pigeons has been known for some time. Nitzsch, in his work on Pterylography, incidentally mentions that in the genus *Goura* there are no cæca to the intestine, and that the gall-bladder is absent. The same facts are noted by Hunter*. The former naturalist also refers to the absence of the oil-gland in the same genus. Prof. Owen says† that the gall-bladder is constantly deficient—a statement which, as will be seen further on, requires some qualification. The fact that all the European species of Doves belong to the genera *Columba*, *Turtur*, and *Pterocles* has caused zoologists to estimate the characters of the whole suborder more from these than from the much larger number found in extra-European countries; and the results arrived at from a more extended study tend considerably to modify the prevailing impression as to the constancy of certain characters.

The differences observable in the following structures have engaged my attention:—

1. The number of rectrices.
2. The presence or absence of the oil-gland, which is never otherwise than nude.
3. The presence or absence of cæca to the intestine, which in no genera, except in *Pterocles* and *Syrnhaptes*, exceed half an inch in length.
4. The presence or absence of the ambiens muscle, which does not seem as yet to have engaged the attention of naturalists, so far as this suborder of birds is concerned.

I. *The number of tail-feathers in the different genera of the Columbæ.*

Nitzsch divides the Pigeons into those with 12 and those with

* Essays and Observations, vol. ii. p. 291.

† Anatomy of Vertebrates, vol. ii. p. 177.

16 rectrices, and does not refer to any other numbers. Different authors have recorded the number of tail-feathers in some of the genera. Twelve, fourteen, sixteen, and twenty are the numbers which I have been able to find in the different species which I have been able to examine, though in *Caloenas* one specimen had only ten rectrices in the perfect tail, whilst most have twelve. Inspection of the following list will show that in some of the genera there are peculiarities in the number of the tail-feathers which indicate difference of more than specific importance; for instance, in *Carpophaga* fourteen is the typical number of the rectrices, but *C. novæ-zealandiæ* differs from all its congeners in possessing only twelve:—

Name of genus and species.	Number of rectrices.
<i>Caloenas nicobarica</i>	12
<i>Chalcopelia puella</i>	12
<i>Chalcophaps chrysochlora</i>	12
<i>Chamæpelina talpacoti</i>	12
<i>Columba</i> (all the species examined)	12
<i>Ectopistes migratorius</i>	12
<i>Leptoptila crumenifera</i>	12
<i>Lopholæmus antarcticus</i>	12
<i>Macropygia phasianella</i>	12
<i>Metriopelia melanoptera</i>	12
<i>Starnænas cyanocephala</i>	12
<i>Turtur</i> (all the species examined)	12
<i>Tympanistria bicolor</i>	12
<i>Zenaida martinicana</i>	12
<i>Carpophaga</i> (all species examined* except <i>C. novæ-zealandiæ</i>)	14
<i>Didunculus strigirostris</i>	14
<i>Geopelia</i> (all species examined)	14
<i>Leucosarcia picta</i>	14
<i>Ocyphaps lophotes</i>	14
<i>Phlogænas cruentata</i>	14
— <i>crinigera</i>	14
<i>Ptilonopus</i> (all species examined except one specimen in Brit. Mus., marked <i>P. occipitalis</i> ♀, with 16)	14
<i>Treron</i> (all species examined)	14
<i>Zenaidura marginata</i>	14
<i>Goura coronata</i>	16
— <i>victoriæ</i>	16
<i>Phaps chalcoptera</i>	16
<i>Pterocles alchata</i>	16
— <i>arenarius</i>	16
<i>Otidiphaps nobilis</i>	20

It will be observed, as has been remarked by Prof. Baird, that, with the exception of *Zenaidura*, all the North American *Columbæ* possess 12 rectrices.

* Including *C. spilorrhoa*, of which I have examined several examples.

II. The presence or absence of the oil-gland in the genera of the Columbæ.

The oil-gland is present in most of the Pigeons; it is very small in the genus *Ptilonopus*. It need hardly be remarked that, when present, it is never tufted.

The oil-gland is present in all the specimens examined by me of

<i>Calœnas,</i>	<i>Metriopelia,</i>
<i>Carpophaga,</i>	<i>Ocyphaps,</i>
<i>Chalcopelia,</i>	<i>Phaps,</i>
<i>Chalcophaps,</i>	<i>Phlogœnus,</i>
<i>Chamœpelia,</i>	<i>Ptilonopus</i> (? in <i>P. melano-</i>
<i>Columba,</i>	<i>cephalus</i>),
<i>Ectopistes,</i>	<i>Pterocles,</i>
<i>Geopelia,</i>	<i>Turtur,</i>
<i>Leptoptila,</i>	<i>Tympanistria,</i>
<i>Leucosarcia,</i>	<i>Zenaida,</i>
<i>Lopholœmus,</i>	<i>Zenaidura.</i>
<i>Macropygia,</i>	

The oil-gland is absent in all my specimens of

<i>Didunculus,</i>	<i>Starnœnas,</i>
<i>Goura,</i>	<i>Treron.</i>

III. The presence or absence of cœca to the intestine in the genera of the Columbæ.

My dissections lead to the result that the intestinal cœca are absent in more genera of Pigeons than they are present in, being found in only 7 out of 26. When present they never exceed a quarter of an inch in length (except in the Pteroclidæ), and are frequently not half that size. In *Turtur* they are generally shorter than in *Columba*.

Cœca are present in

<i>Columba,</i>	<i>Pterocles,</i>
<i>Ectopistes,</i>	<i>Starnœnas,</i>
<i>Macropygia,</i>	<i>Turtur.</i>
<i>Phlogœnas,</i>	

Cœca are absent in

<i>Calœnas,</i>	<i>Lopholœmus,</i>
<i>Carpophaga,</i>	<i>Metriopelia,</i>
<i>Chalcopelia,</i>	<i>Ocyphaps,</i>
<i>Chalcophaps,</i>	<i>Phaps,</i>
<i>Chamœpelia,</i>	<i>Ptilonopus,</i>
<i>Didunculus,</i>	<i>Treron,</i>
<i>Geopelia,</i>	<i>Tympanistria,</i>
<i>Goura,</i>	<i>Zenaida,</i>
<i>Leptoptila,</i>	<i>Zenaidura.</i>
<i>Leucosarcia,</i>	

IV. *The presence or absence of the ambiens muscle in the genera of the Columbæ.*

This muscle, of which the slender tendon runs in such a peculiar manner obliquely across the knee, arising from the supero-anterior margin of the acetabulum, and inserted into the muscular fibres of the flexor perforatus of the toes, is found in the greater number of the Pigeons I have examined, being present in about three fourths of the genera.

The ambiens muscle is present in

<i>Calœnas,</i>	<i>Lopholæmus,</i>
<i>Carpophaga,</i>	<i>Macropygia,</i>
<i>Chalcopelia,</i>	<i>Metriopelia,</i>
<i>Chalcophaps,</i>	<i>Ocyphaps,</i>
<i>Chamæpelia,</i>	<i>Phaps,</i>
<i>Columba,</i>	<i>Pterocles,</i>
<i>Didunculus,</i>	<i>Turtur,</i>
<i>Ectopistes,</i>	<i>Tympanistria,</i>
<i>Leptoptila,</i>	<i>Zenaida,</i>
<i>Leucosarcia,</i>	<i>Zenaidura.</i>

The ambiens muscle is absent in

<i>Geopelia,</i>	<i>Ptilonopus,</i>
<i>Goura,</i>	<i>Starœnas,</i>
<i>Phlogœnas,</i>	<i>Treron.</i>

The combination of the above-collected facts ought to be of considerable service in any attempts at classification; for, leaving the number of rectrices out of the question for the minute, of the eight possible variations of the three remaining characters, there are seven which are found to exist; in other words there are Pigeons known—

(1) With an oil-gland, cæca, and an ambiens muscle, viz. *Columba*, *Ectopistes*, *Macropygia*, *Pterocles*, and *Turtur*.

(2) With an oil-gland, no cæca, and an ambiens muscle, viz. *Calœnas*, *Carpophaga*, *Chalcopelia*, *Chalcophaps*, *Chamæpelia*, *Leptoptila*, *Leucosarcia*, *Lopholæmus*, *Metriopelia*, *Ocyphaps*, *Phaps*, *Tympanistria*, *Zenaida*, and *Zenaidura*.

(3) With no oil-gland, no cæca, and an ambiens muscle, viz. *Didunculus*.

(4) With an oil-gland, cæca, and no ambiens muscle, viz. *Phlogœnas*.

(5) With no oil-gland, cæca, and no ambiens muscle, viz. *Starœnas*.

(6) With an oil-gland, no cæca, and no ambiens muscle, viz. *Geopelia*, *Ptilonopus*.

(7) With no oil-gland, no cæca, and no ambiens muscle, viz. *Treron*, *Goura*.

The only combination not found being that (8) in which, of the three structures concerned, the oil-gland only is wanting.

The relative value of these different structural peculiarities is the point on which their value in classification evidently hinges. The number of rectrices being the most variable of them, its importance

is most probably the least. Next, with regard to the oil-gland, it is evident that genera such as *Treron* and *Ptilonopus* are not very far separated, notwithstanding that there are important differences between them; yet the former wants the oil-gland and the latter possesses it, though but feebly developed in *P. jambu* and *P. mariæ*, and absent (apparently) in *P. melanocephalus*. It is also known that among the Psittaci this structure may or may not be developed. These considerations lead me to think that less stress should be laid on the oil-gland than on the two following characters.

The constancy of the cæca, as a point of more than family importance in all other birds, would lead me to consider their presence or absence as more significant than that of the oil-gland.

In my last communication to this Society* I gave reasons to show that the presence or absence of the ambiens muscle was a very significant fact in the classification of birds generally. This would lead me to lay considerable stress on the same point in any order or sub-order in which it is found to vary.

Assuming then, as in my last paper, for reasons there stated, that the ancestral Pigeon possessed the ambiens muscle, and, on the same grounds, that it had cæca coli and an oil-gland, it is evident that the Pteroclidæ, together with *Columba*, *Turtur*, *Macropygia*, and *Ectopistes* have departed least from the ancestral type. The Pteroclidæ have branched off in another direction, as will be subsequently shown; and therefore *Columba*, *Turtur*, *Ectopistes*, and *Macropygia* (together with those undissected genera unmistakably allied to them) may be considered to be the least modified, and therefore most typical of the Columbæ.

From these, if the peculiarities of the ambiens muscle have the importance which I assign them, a branch sprang, in which the ambiens was undeveloped. This includes at the present day *Starænas*, *Phlogænas*, *Geopelia*, *Ptilonopus*, *Treron*, and *Goura*, most of which possess 14 rectrices, and are confined to the Malay archipelago. This *Treronine* division, as it may be termed, seems to be preserved in its primitive form in *Phlogænas*, in which no further structures are lost. *Starænas*, which, notwithstanding its peculiar distribution, must be considered as a member of it, loses the oil-gland, and *Geopelia*, as well as *Ptilonopus*, the cæca, whilst *Treron* and *Goura* are deficient in both.

The main stem seems to have shortly given off a second branch, in which the cæca coli were alone wanting. This Phapine branch is now represented, without further complication, by *Calænas*, *Carpophaga*, *Chalcopelia*, *Chalcophaps*, *Chamæpelia*, *Leptoptila*, *Leucosarcia*, *Metriopelia*, *Ocyphaps*, *Phaps*, *Tympanistria*, and *Zenaida*; whilst from it has sprung *Didunculus*, without any oil-gland and with its quaint beak and remarkably long intestinal canal, which would indicate that its diet was usually one of fish, or more probably mollusca†.

* P. Z. S. 1874, p. 111.

† It is through the kindness of Prof. Newton that I have had the opportunity of dissecting a specimen of this rare bird.

Respecting *Lopholæmus*, it may be mentioned that the only opportunity I have had of dissecting it has been through the kindness of Mr. Edward Gerrard, who lent me two specimens, not well preserved, in spirit*. In these I could not find the least trace of the accessory femoro-caudal muscle, which is well developed in all other Pigeons. This peculiarity, when taken in connexion with the fact that, like *Carpophaga* only amongst the Phapinæ, it possesses a gall-bladder, makes me disposed to make it an independent minor branch from the *Carpophagine* stem.

Most ornithologists seem to be very unwilling to place the Pteroclidæ along with the true Pigeons in a single group, notwithstanding the evidence brought forward by Nitzsch, and the statement of M. Blanchard. My own observations tend to show that the two families are most intimately related, and that they must be most certainly included in the same suborder, though forming two quite independent families.

Commencing with the osteological evidence on this point, which has been very fully discussed by Mr. Parker and Prof. Huxley, the skull presents strong Columbine features. The pterygoid bones are peculiarly curved, in a manner seen nowhere else but among the Pigeons; and as in them, and not in the Fowls, the basipterygoid facets are situated midway between their two extremities. The nasal bones are, no doubt, peculiar; they are not at all typically schizorhinal, but present the extreme degree of modification of that type, probably the result of the shortness and breadth of the beak. There is, however, a nasal turbinal bone, partly occluding the osseous external nares, as in the Pigeons, whilst the premaxillary process of the nasal bone is also of considerable length. The palatine bones are perfectly Columbine in some species (e. g. *Pterocles arenarius*), and are not much modified in others, never so much so as are those of *Didunculus*. In the lower jaw there is no produced and upturned angle, like that in the Gallinæ. The cranial articular end of the quadrate bone is also strongly bifurcate. The whole skull seems to be that of a Pigeon modified by the effects of a Grouse-like life.

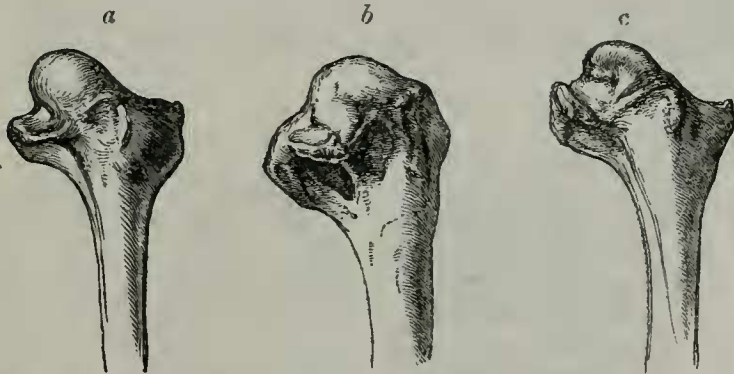
The furcula has no median symphysial plate or hypocleidium. The sternum is perfectly Columbine, the similarity extending to the direction taken by the costal processes and the non-development of any true manubrial rostrum, in both which points the Gallinæ are so different.

The head of the humerus presents an important character. From any number of birds' humeri those of the Columbæ may be identified, if those of the Psittaci are excluded, because the pectoral lamina or the ridge for the insertion of the great pectoral muscle is peculiar. In most birds the second pectoral muscle is inserted into

* An additional specimen has come into my hands since the above was written, by which the accuracy of my previous dissections of the species is confirmed. No accessory femoro-caudal was present; there were no cæca coli; there was a large elongated gall-bladder and a small oil-gland. The gizzard was remarkably small, with irregular pads, one of which somewhat resembled that of *Ptilonopus*.

the proximal end of this ridge, or into a prolongation of it. In the Columbæ, Psittaci, and Alcidae this is not the case; for in them it has quite an independent place of insertion into the general surface of the head of the bone at some distance from the pectoral ridge. An oval roughness indicates the spot. It is at the angle formed by the pectoral ridge and the main part of the bone in the Gallinæ, but nearer the other side of the bone in the Columbæ. A glance at the bone itself or the accompanying drawing of it (fig. 1) will explain the point more than any amount of description. It will also be

Fig. 1.



Heads of right humerus of:—*a. Pterocles arenarius*; *b. Gallus bankiva*;
c. Columba livia.

found that the pectoral ridge in the Columbæ and some of the Psittaci ends proximally in a point, peculiar to them. The Pteroclidæ agree exactly with the Pigeons in all these points, and differ widely from all the Gallinæ.

In all important features the pelvis of the Pteroclidæ differs with the Columbæ from the Gallinæ, as in having no strongly marked fossa on the inner surface of the ischium; but in the slight development of the transverse processes of some of the sacral vertebræ it is peculiar.

The general proportions of the muscles in the Pteroclidæ are perfectly Columbine. The pectoral muscles are similarly disposed, and the crop rests on the proximal surface of the great pectoral in a similar manner. In the leg the same resemblance maintains. Among muscles the ambiens, the femoro-caudal (A), the accessory femoro-caudal (B), the semitendinosus (X), and the accessory semitendinosus (Y) are all present in Columbæ and in Gallinæ, which prevents any difference in myological formula* from assisting in distinguishing them. In the obturator internus muscle a well-marked contrast between the Pigeons and Fowls is observed, which also shows that *Pterocles* is one of the former. In *Columba* and the whole suborder this muscle is small, narrow, and elliptical; but in *Gallus* and all its

* See P. Z. S. 1874, p. 111.

allies it is triangular and very large at its base. The similar number of carotid arteries in the Columbidae, Pteroclidæ, and Gallinæ prevents any inference being drawn from them; and the same may be said of the œsophageal crop.

In the cæca of the intestine in the Pteroclidæ there is, no doubt, a strong likeness to the Gallinæ; for whilst, as above shown, they are very short or absent in the Columbæ, they are voluminous and long in the Sand-Grouse and Fowls, being in the former between 4 and 5 inches from end to end. As in all the Gallinæ and some Columbæ (*Carpophaga* and *Ptilonopus*), the Pteroclidæ possess a gall-bladder.

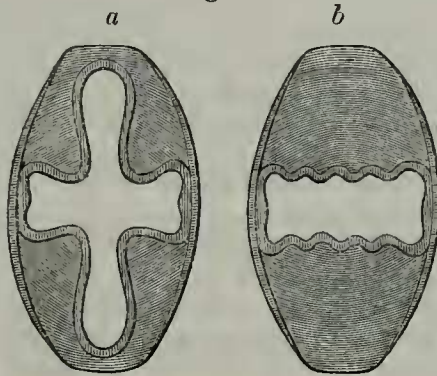
The following Table gives the length of the intestine, from the gizzard to the cloaca, in the species named. The most peculiar point to be noticed is its excessive length in *Didunculus*:—

Name of bird.	Length of intestine.	
	ft.	in.
<i>Carpophaga aurora</i>	1	10
— <i>cenea</i>	1	6
<i>Chalcopelia chalcospilos</i>	1	6
<i>Chalcophaps chrysochlora</i>	1	8½
<i>Columba maculosa</i>	2	8
<i>Didunculus strigirostris</i>	7	0
<i>Ectopistes migratorius</i>	2	6
<i>Geopelia cuneata</i>	0	8½
— <i>humilis</i>	1	6
— <i>placida</i>	1	1
— <i>striata</i>	0	11½
<i>Goura coronata</i>	5	1
— <i>victoriæ</i>	4	0
<i>Lopholæmus antarcticus</i>	1	4½
<i>Macropygia phasianella</i>	2	8
<i>Metriopelia melanoptera</i>	2	0
<i>Ocyphaps lophotes</i>	2	3
<i>Phaps chalcoptera</i>	2	6
<i>Pterocles alchata</i>	1	6
— <i>arenarius</i>	2	1
<i>Ptilonopus jambu</i>	1	0
— <i>marie</i>	0	11
— <i>melanocephalus</i>	0	9
<i>Starnænas cyanocephala</i>	2	10
<i>Treron calva</i>	2	4½
<i>Turtur aldabranus</i>	1	8
— <i>chinensis</i>	1	6
<i>Zenaida martinicana</i>	1	11
<i>Zenaidura carolinensis</i>	2	0

In nearly all Pigeons the gizzard is well-developed after the ordinary type; in some the pad on which the food is triturated is longitudinally grooved or plicated, whilst in others it is smooth; its

ossification in the Nicobar Pigeon (*Caloenas nicobarica*) has already attracted attention*. In *Carpophaga* the stomach is very feebly muscular, not being more powerful than in strictly fruit-eating birds, such as the Hornbills. It is in the genus *Ptilonopus* that a form of gizzard is developed *such as is not found in any other bird*. In *P. mariæ*, *P. melanocephalus*, and *P. jambu* it is exactly the same, being composed of four pads instead of two. A horizontal section of an ordinary gizzard presents the well-known section represented in fig. 2, *b*, it being composed of two muscular masses, which push the two pads together in a manner which I have explained elsewhere†. But in *Ptilonopus* the section is much more elaborate, in a direction to which no other gizzard is known to approach; so that by the gizzard alone the genus whence it came could be determined with certainty. The accompanying figure (*a*) represents the section made exactly in the

Fig. 2.



Horizontal section of the gizzard of:—*a. Ptilonopus jambu*; *b. Treron calva*.

same direction as in the former case; and from it the four longitudinal muscular masses, which are here seen cut across, are well displayed, leaving a cruciform cavity between them, through which the food passes whilst being triturated. This gizzard is small in proportion to the size of the bird. No approach to a like condition is to be observed in *Treron*, the section of the gizzard in that genus being quite of the ordinary form figured above.

It is generally said that the gall-bladder is absent in the Columbæ; and this is so in most of them; but besides being developed in the Pteroclidæ, it is found in all the species of *Ptilonopus*, *Lopholæmus*, and *Carpophaga*. In this point also *Ptilonopus* therefore differs from *Treron*.

The following Table contains the names of the different genera of the Columbæ arranged in the manner suggested above. As a classification of the suborder it is not at all my desire to put it forward as an ultimate one, but simply as the expression of the known facts of

* See Prof. Flower's observations, P. Z. S. 1860, p. 333, and Mr. Bartlett's note, *ib.* p. 99.

† P. Z. S. 1872, p. 525.

their structure. A more extended series of observations may indicate reasons for modifying the stress laid on some of the points; but it cannot, if my dissections are correct, change the facts themselves. As an instance of the direction in which alterations may be shown to be required, the case of the relation of *Ptilonopus* and *Treron* may be taken; for, notwithstanding their general similarity in structure, these two genera present important points of difference. In the possession of a gall-bladder by the former, it resembles *Carpophaga*; and it is quite possible that the similarity of the two genera under consideration is the result of similarity in habit only, and that whilst the latter (*Treron*) sprang from the Treronine stem direct, the former (*Ptilonopus*) may have descended from the Phapine stock. This appearance of the gall-bladder in these genera is very difficult to explain, except on the supposition that in those in which it is absent it has been lost very lately, or that *Carpophaga* and *Ptilonopus* are very intimately related forms. The uncertainty of its appearance in closely related genera of Mammalia reduces its value as a character of classificational importance among them; but its very general absence in the Columbæ makes it almost impossible not to lay considerable stress, in classification, on its presence. In the accompanying Table *Ptilonopus* is placed in the same division with *Treron* because of their similarity in the points there laid stress on; but it requires a very inconsiderable amount more evidence to necessitate its being removed from there into close proximity with *Carpophaga* and *Lopholæmus*. The fact that two forms in many respects so similar should differ so much in others is of itself a strong argument in favour of their separation; for the probability that forces which tend to produce marked external resemblances should simultaneously develop internal differences is, to say the least, extremely small.

Suborder COLUMBÆ. Schizorhinal birds with a characteristic pterylosis, humerus-head, and sternum; with the fourth gluteal muscle, which in other schizorhinal birds covers the femur-head, undeveloped; with the oil-gland nude, when present, and with the gall-bladder generally absent.

Family COLUMBIDÆ. Columbæ in which the intestinal cæca never exceed half an inch in length.*

Subfamily COLUMBINÆ. Columbidae possessing the ambiens muscle, intestinal cæca, an oil-gland, no gall-bladder, and 12 rectrices.

Genus *Columba*.

„ *Turtur*.

„ *Macropygia*.

„ *Ectopistes*.

Subfamily PHAPINÆ. Columbidae possessing the ambiens muscle and no intestinal cæca.

Division α . The oil-gland present, no gall-bladder.

Genus <i>Chamæpelis</i> .	}	American.
„ <i>Metriopelia</i> .		
„ <i>Zenaida</i> .		
„ <i>Zenaidura</i> .		
„ <i>Calænas</i> .	}	Old-World.
„ <i>Chalcopelia</i> .		
„ <i>Tympanistria</i> .		
„ <i>Ocyphaps</i> .		
„ <i>Leucosarcia</i> .		
„ <i>Phaps</i> .		

Division β . The oil-gland and gall-bladder present.

Genus *Carpophaga*.

Division γ . The accessory femoro-caudal muscle absent (it being present in all other Columbæ); the oil-gland and gall-bladder present.

Genus *Lopholæmus*.

Division δ . The oil-gland and gall-bladder absent.

Genus *Didunculus*.

Subfamily TRERONINÆ. Columbidae wanting the ambiens muscle.

Division α . With intestinal cæca and an oil-gland; no gall-bladder.

Genus *Phlogœnas*.

Division β . With intestinal cæca, no gall-bladder, and no oil-gland.

Genus *Starnœnas*.

Division γ . With an oil-gland, no gall-bladder, and no intestinal cæca.

Genus *Geopelia*.

Division δ . With no intestinal cæca, no oil-gland (or a very small one), and scutellated tarsi.

Genus *Treron*.

„ *Ptilonopus*.

Division ϵ . With no intestinal cæca, no oil-gland, no gall-bladder, and tarsi reticulate.

Genus *Goura*.

Family PTEROCLIDÆ. Columbæ in which the intestinal cæca considerably exceed half an inch in length.

Subfamily PTEROCLINÆ. Pteroclidæ possessing the ambiens muscle, a gall-bladder, and an oil-gland.

Genus *Pterocles*.

„ *Syrrhaptes*.